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EDITORIAL

# The functional ecology of plant silicon: geoscience to genes

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Silicon (Si) is now widely recognized to benefit plants through protection against a range of biotic and abiotic stresses, including herbivory, pathogen attack and climatic fluctuations. But this recognition has been a long time in the making and, like many ecological histories, it links back to Darwin. Silica ($SiO_2$) phytoliths were identified in dust samples collected by Darwin on the HMS Beagle voyage in 1833; they were sent to Germany and named *phytolitharia* by Christian Ehrenbeg in 1835 (Piperno 2006). Agricultural researchers were perhaps quicker to recognize the importance of plant silicon than evolutionary biologists or ecologists. A functional role for Si, namely that of protecting crop plants against herbivory, was identified in agricultural systems almost a century ago (McColloch & Salmon 1923), and now Si treatments are routinely applied to protect crops from herbivore attack and increase yields (Keeping & Reynolds 2009; Guntzer, Keller & Meunier 2012; Reynolds *et al*. 2016). In contrast, relatively less attention was given to the role of Si in ecology, despite some seminal papers predicting its importance (Sangster 1978; Iler 1979; Raven 1983; Parry *et al*. 1984; Sangster & Hodson 1986; Takahashi, Ma & Miyake 1990; Epstein 1994, 1999). These papers highlighted the high levels of Si in soils, its prominence in many plant families, but a lack of research on its functional roles by experimental plant biologists.

Si research began to re-focus towards ecology in the 1980s, with the pioneering work of McNaughton and Tarrants demonstrating the inducibility of Si defences in response to herbivory (McNaughton 1985; McNaughton *et al*. 1985). However, the importance of Si in plant ecology, or even in mediating plant–herbivore interactions, did not gain real traction or prominence for another twenty years. This may be partially because Si defences are most important in grasses, for which tolerance is often regarded as a more prevalent strategy than active defence. Vicari & Bazely (1993) re-emphasized the importance of recognizing Si defences in studies of grass-grazer interactions. Subsequently, a series of papers by Hartley and colleagues (Massey, Ennos & Hartley 2006, 2007b; Massey & Hartley 2006, 2009; Massey *et al*. 2009) describing the induction of Si defences in wild grass species, their effects on the palatability and digestibility of plants, and consequences for the performance of herbivores inspired a surge in studies investigating the functional role of Si in natural ecosystems (e.g. Soininen *et al*. 2013; Huitu *et al*. 2014; Quigley & Anderson 2014). Exciting developments include an improved understanding of the impacts of Si on mammalian teeth (Calandra *et al*. 2016) and an elucidation of the physiological mechanisms by which Si limits nutrient absorption by mammals (Wieczorek *et al*. 2015). There is also increasing evidence for a role of Si in determining the population dynamics of herbivores (Reynolds *et al*. 2012; Wieczorek *et al*. 2015).

The idea that Si is essential to our understanding of plant ecology is burgeoning. Cooke & Leishman (2011a) reviewed the diverse ecological functions of Si and argued for greater consideration in plant ecology. Establishing the ecological role of Si in a theoretical framework includes an integration into the leaf economic strategy (Cooke & Leishman 2011b), evaluating Si defences within the context of broadly applied ecological theories such as the Resource Availability Hypothesis (Massey, Ennos & Hartley 2007a) and understanding plant Si accumulation strategies (Cooke & Leishman 2012; Carey & Fulweiler 2014). The compilation and analysis of diverse plant Si concentrations by Hodson *et al* (2005) highly cited as it facilitated explorations of phylogenetic variation in Si accumulation. Ecological studies were also expedited by recent discoveries of the biochemical and molecular mechanisms underlying the uptake and expression of Si in crop and wild plant species, which have explained the variation in the quantity of Si plants acquire and how it is distributed (Ma *et al*. 2004; Ma & Yamaji 2015). Another key to the expansion of ecological studies was new technologies to rapidly and cheaply quantify plant Si concentrations, allowing sufficient replication to quantify the variation at scales relevant to ecological research (Reidinger, Ramsey & Hartley 2012; Smis *et al*. 2014).

Plants have had significant impacts on biomineralization of Si and weathering rates over geological time-scales (Conley & Carey 2015; Trembath-Reichert *et al*. 2015),

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form an important reservoir in the global Si budget and exert control on biogeochemical cycles (Conley 2002; Struyf *et al*. 2009). Some ecosystem-scale Si cycles have been described (e.g. Bartoli 1983; Struyf & Conley 2008; Cornelis *et al*. 2009), and we now appreciate the relevance of Si to other cycles such as C, N and P, particularly in the context of agricultural production (Li, Song & Cornelis 2014). Thus, Si is not just a useful element for plants but, in addition, plants have had a huge impact on the global Si biogeochemical cycle, perhaps even to a similar extent to their effects on C and O pools and fluxes on earth. There is now urgency to understand the responses of plant Si to environmental stresses under predicted climate change scenarios (Fulweiler *et al*. 2015) and the implications for vital ecosystem services and food security.

There has been a long history of plant Si research, but the field has really taken off, particularly in terms of ecological functions for Si, within the last two decades. It is now timely to take stock and draw together the latest research on plant Si and take advantage of emerging synergies between seemingly disparate fields, ranging from the molecular to the geological, to shape clear directions for future studies.

## The current status of plant silicon research in ecology

This special feature of *Functional Ecology* aims to consolidate current understanding from a plant functional perspective, encompassing all scales, from geosciences to genes, tracing Si in both soils and plants and fusing knowledge from individual studies into powerful generalized statements. Exploitation of plant Si use for agricultural gain and palaeontological research are valuable applied aspects of, and contributors to, plant Si knowledge. We frame this issue from an ecological viewpoint to better understand plant Si evolution, ecological interactions and ecosystem applications.

Epstein (1994) noted that Si accumulation was highly variable both within and between plant species and families; possibly the element accrued most variably by plants. We seek to understand this variation in Si accumulation and its consequences – why do some families/species/genotypes/plants use Si more than others, and what are the fitness benefits that it confers? Deshmukh & Belanger (2016, *this issue*) review molecular evidence of Si uptake, and Stromberg, Di Stillo & Zhaoliang (2016, *this issue*) search for evidence of adaptive origins. Cornelis & Delvaux (2016, *this issue*) examine the relationship between soil development and plant Si cycling, while Hartley & DeGabriel (2016, *this issue*) review how Si uptake mediates the interactions between plants and their herbivores, focussing on natural ecological systems. Schoelynck & Struyf (2015, *this issue*) interpret the findings from wetland studies, where structural function is best understood and Si accumulation varies with functional type. Finally, Carey & Fulweiler (2015, *this issue*) assess the implications of Si uptake in agriculture and therefore global Si cycling, and Cooke & Leishman (2016, *this issue*) synthesize many studies to show how plants consistently use Si in abiotic stress alleviation despite between-family Si variation. Below, we highlight the key findings.

### ADVANCES IN GENOMICS ARE IMPROVING OUR ABILITY TO PREDICT WHICH SPECIES ACCUMULATE SI

Deshmukh & Belanger (2016) describe progress in understanding the molecular mechanisms that underlie Si uptake in plants, demonstrating that by identifying sequences encoding these transporters, genomic data allow the prediction of accumulation capacity and therefore the species likely to benefit. The presence of a passive Si influx transporter (nodulin 26-like intrinsic proteins, NIPs, part of an ancient family of aquaporins) identifies plants as Si competent, as they are permeable to silicic acid. Accumulation also requires an efflux transporter belonging to a less-studied family of putative anion transporters, thought to be actively driven by proton gradients, which have been identified in few species. In general, as shown in the dominant model, rice, silicic acid is taken up in the exodermis by Lsi1 (Ma *et al*. 2006) and released by Lsi2 (Ma *et al*. 2007), where Si then diffuses through the apoplast of the parenchyma. Genes encoding these membrane-bound transporters are highly conserved across species and entirely different to the transporters in diatoms which also accumulate Si.

### THERE IS NO CONVINCING EVIDENCE FOR GRASS-GRAZER CO-EVOLUTION MEDIATED BY SI

Stromberg, Di Stillo & Zhaoliang (2016, *this issue*) attribute the diversity in Si accumulation across families to the longevity of the relationship between vascular plants and Si in the environment as well as utilization strategies. Distinguishing discrete plant silica bodies (phytoliths) from plant Si, they examine the evolution of phytolith function, searching for adaptive origins. Strömberg *et al*. consolidate debate on the capacity of phytoliths to abrade herbivore teeth and mouthparts, concluding that it does cause wear, but query the magnitude of phytolith damage in comparison with grit. By mapping silica content data on to time-calibrated land plant (specifically grass) phylogenies, they show that silica accumulation evolved multiple times rather than being an ancestral trait, consistent with adaptive hypotheses. Finally, they compare the dates when high accumulating species evolved with periods when Si accumulation is hypothesized to have been advantageous, such as when specific herbivore groups evolved. Significantly, no convincing proof for Cenozoic grass-grazer co-evolution was found, an important advance here, flagging this area as ripe for further research.

### THE ROLE OF SOIL-BASED FACTORS IN SI ACCUMULATION IS CRUCIAL

Cornelis & Delvaux (2016, *this issue*) examine both the influence of plants on soil weathering and conversely, the

weathering status of soil on Si availability for plants. The authors argue that as soils develop, first lithogenic and pedogenic silicates are the source of Si for plants, but over time this source is depleted; instead, the Si in soils has mostly already cycled through plants and exists as phytogenic silicates. As phytoliths are more soluble than inorganic silicates, the rate at which Si accumulates, and is recycled by vegetation, is more rapid in more developed soils. This highlights the role of soil development in the accumulation of Si by plants at an ecosystem scale, potentially allowing predictions of Si cycles in novel ecosystems based on soil classification.

## SI IS AN EFFECTIVE PLANT DEFENCE AGAINST A RANGE OF HERBIVORES

Hartley & DeGabriel (2016) provide a comprehensive review of one of the best studied functions of Si, antiherbivore defence. They focus on ecological studies in grasses, and both insect and mammalian herbivores. Si-containing structures make leaves abrasive, reducing palatability and decreasing digestibility by reducing nitrogen acquisition. In species where Si defences can be upregulated, a threshold of herbivore damage is needed for induction but artificial clipping does not elicit the same response. Hartley and DeGabriel observe that Si defences have differing impacts on different types of herbivores, and suggest that this is likely a function of body size, feeding behaviour and digestive physiology. They highlight the predominance of laboratory studies and the inherent difficulties of studying Si in natural ecosystems. Nevertheless, they provide new evidence that Si uptake in the field requires a threshold level of grazing damage and demonstrate that, regardless of damage, Si levels fluctuate seasonally. Hartley and DeGabriel clearly demonstrate the ecological importance of silicon as an herbivore defence, though the interactions between plants, their environment and their herbivores are undoubtedly complex.

## SI ACCUMULATION IS A FUNCTIONAL TRAIT IN WETLAND ECOSYSTEMS

Schoelynck & Struyf (2015, *this issue*) contend that Si accumulation in wetland species has adaptive capacity for environmental conditions. Many macrophytes are high Si accumulators, in part because abundant water allows high transpiration rates. Schoelnyck and Struyf show the variation in Si accumulation between plant functional groups, with rooted and emergent species higher Si accumulators than free-floating and plants with floating leaves. However, most species appear plastic and vary in Si accumulation in response to water, wind, herbivory and nutrient stress. One of the purported functions of plant silicon is as a structural component (Raven 1983), and Schoelnyk and Struyf collated the relationships between Si accumulation and lignin and cellulose which have been best studied in aquatic plants. Results are puzzling, with significant relationships found within species or plant groups, but without consistency across studies, possibly due to methodological differences. Schoelynk and Struyf compile evidence of roles in herbivore defence, structure, stress alleviation, litter dynamics and biogeochemical cycling for wetlands, one of few ecosystems where multiple functions of silicon have been studied in any detail, which sets a promising trend for other ecosystems.

## AGRICULTURAL PRODUCTION IS ALTERING GLOBAL SI CYCLES

Carey & Fulweiler (2015) estimate that agricultural crops account for a staggering ~35% of biogenic Si uptake, due to the comparatively large biomass of agricultural plants, and because 6 of the 10 most productive crops are high Si-accumulating species. This is in addition to previously described changes in Si cycles caused by human activity (Conley *et al*. 2008; Clymans *et al*. 2011). Si accumulation by agricultural crops has tripled in the last 50 years, and will increase a further 22–35% by 2050, suggesting further human-derived perturbations in the Si cycle in future (Carey & Fulweiler 2015). Because plant-derived Si is more soluble than lithogenic Si, agricultural production is increasing the amount of labile Si in some areas, but decreasing it in instances where biomass is harvested and transported elsewhere. Both have implications for Si availability in rivers and oceans. By highlighting how agriculture impacts the global Si cycle similar to the P cycle (soil depletion) and N cycle (loss through leaching and run-off), the authors affirm that Si cannot be ignored in agriculture.

## SI IS IMPORTANT IN PROTECTING PLANTS AGAINST ABIOTIC STRESS

Cooke & Leishman (2016, *this issue*) used meta-analytic methods to compile data from agricultural studies on Si addition to stressed plants and examine the patterns among species. Si is applied as a fertilizer for many crops as it alleviates a broad range of abiotic stresses, though previous research has focused on the benefits of Si for a single species. The authors show that across studies Si alleviates oxidative damage in stressed plants and increases plant dry weight, chlorophyll biosynthesis and assimilation rate. Several mechanisms are involved, and stress alleviation varies with stress type. While herbivory can induce an increase in Si accumulation, abiotic stress does not consistently increase Si uptake, and may instead generally reduce Si accumulation in shoots. A role for Si in stress alleviation has rarely been studied in ecology (but see Struyf & Conley 2008; Querné, Ragueneau & Poupart 2012). Cooke and Leishman provide strong evidence, through consistent responses of stressed plants to Si across diverse species and stresses, that Si plays important roles in plant fitness that we do not yet appreciate.

## Future directions for understanding the ecology of plant silicon

Throughout this issue, we seek to identify key knowledge gaps that currently prevent a full understanding of the functional ecology of plant Si. A key issue is clearly scale: so many experimental studies have been conducted on individual plants or groups of plants in pots, plots and glasshouses, and we urgently need landscape-scale studies, whether that is to address the role of Si in plant–herbivore interactions, or to assess potential fitness benefits of Si accumulation by plants. For example, we really have no idea of the importance of Si in alleviating abiotic stresses in natural systems. Experimentation on this scale is challenging, but it is increasingly feasible given new methods of measuring Si rapidly and accurately (e.g. Reidinger, Ramsey & Hartley 2012) and tracing Si movement using isotopes (e.g. Frings *et al*. 2016).

A second challenge is contingency: the outcomes of many experiments on Si-mediated effects appear critically dependent on aspects of the study system, such as soil type, plant and animal species chosen or the methods used to apply and/or measure Si. As we accumulate more studies, we can combine those with techniques like systematic reviews and meta-analyses (see Cooke & Leishman 2016, *this issue*), though more effective communication between Si researchers from different disciplines will also help. Indeed, the diversity of methods and terms used in these multidisciplinary reviews highlights the need for standards to be established for this field. We propose beginning with terminology, as different types of plant Si are currently referred to in multiple ways and present a nomenclature (Table 1) to facilitate knowledge transfer between different disciplines studying Si and better manage challenges of contingency.

It is not just ecological and methodological issues that complicate studies of Si – some of our biggest gaps in understanding relate to the physical environment and its impacts on plant ability to accumulate Si. The role of soil-based factors in Si accumulation is crucial, but under-researched: remarkably, relatively little is known about the Si fluxes between soil and plants, nor about the most important Si pools used by plants (Gocke *et al*. 2013). Another knowledge gap is how Si availability is affected by the soil microbial community or by soil fauna, although recent studies are beginning to address this (Alfredsson *et al*. 2016). Plant Si uptake can be increased by mycorrhizal fungi (Kothari, Marschner & Romheld 1990), and

**Table 1.** Preferred nomenclature for siliceous species associated with plant silicon research

| Preferred name | Symbol | Description/definition | Other names used in the literature |
|---|---|---|---|
| Silicon | Si | The element silicon. Also a generic term used when silicon form/function not specified or for simplification. | Sometimes incorrectly used interchangeably with silica; caution should be taken to specify Si vs. $SiO_2$ |
| Silica | $SiO_2$ | Silicon combined with oxygen ($SiO_2$), often hydrated ($SiO_2.nH_2O$ or $SiO_2.xH_2O$). It exists as several minerals and can be in solid or gel form, with a crystalline or amorphous structure. In plants, silica is amorphous and in discrete bodies, it forms phytoliths. | Silicon dioxide |
| Dissolved silicon | DSi | Silicon combined with oxygen and hydrogen, commonly represented as $H_4SiO_4$ or $Si(OH)_4$ Found in the soil solution, rivers and oceans and is the form taken up by plants and animals. Many Si fertilizers dissolve to supply silicic acid. | Silicic acid, orthosilicic acid |
| Biogenic silica | BSi | Silica formed in plants and animals | Biosilica, sometimes used to describe PhSi when only plants are being discussed |
| Phytogenic silica | PhSi | Biogenic silica specifically produced in plants. Include phytoliths, but also smaller, less discrete deposits in plants. | Plant silica, phytoliths |
| Zoogenic silica | ZSi | Biogenic silica produced in animals, mainly diatoms. | |
| Inorganic silicates | | $SiO_4^{4-}$ -based materials with inorganic origins | |
| Lithogenic silicates | LSi | Silicates originating from silicate minerals and crystals | |
| Pedogenic silicates | PSi | Silicates formed in soils, often from amorphous silica | |
| Amorphous silica | ASi | Non-crystalline silica, from either biogenic or pedogenic sources | At times used to mean BSi, but this is not recommended |
| Human-appropriated biogenic silica | HABSi | BSi in agriculture | |

the mechanisms by which this might occur are becoming clear: AMF can increase the expression of plant aquaporin transporters (Uehlein *et al*. 2007), while similar aquaporins have recently been identified in the fungi themselves (Li *et al*. 2013). Intriguingly, earthworms have now been shown to change the availability of silicic acid (Bityutskii, Kaidun & Yakkonen 2016).

Another environmental factor frequently shown to be important in Si uptake is water availability, whether in the soil or in terms of plant transpiration rates. Si can only enter plants via the roots in solution as silicic acid, and the principle transporter for Si has been identified in many (though largely crop) plant species as a passive aquaporin-based transporter (reviewed by Ma & Yamaji 2015). But key issues remain unresolved (Hartley 2015), most notably that plant–water relations cannot explain the significant observations on Si uptake, such as the recent study which demonstrated that soil water availability affected Si levels in the roots of plants, but not the shoots (Wieczorek *et al*. 2015). Similarly, can deposition really just be about accumulation at transpiration termini when we see dramatically increased Si uptake in response to herbivory, and that such uptake can result in very localized deposition in particular structures on the leaf surface (Hartley *et al*. 2015)? How is this achieved and how is Si distribution between tissue types controlled? It is hard for us to answer those questions in relation to leaf tissue, but even less is known about Si accumulation in other plant tissues, such as stems and bark. Attention is turning to Si deposition in roots, not least because of its potential role in alleviating the increasing problem of root-feeding natural enemies (Johnson, Erb & Hartley 2016).

Advances in molecular and genomic approaches offer promising new avenues in Si research. We now need genomic data for non-agricultural species to better understand how accumulation capacity relates to different Si functions (e.g. abiotic stress alleviation vs. herbivore defences), particularly in species that only accumulate small amounts of Si but still see benefits (Cooke & Leishman 2016, *this issue*). In addition, we still lack a definitive method for classifying plants in terms of their Si accumulation capacity, with silicon accumulation as a continuous trait more realistic for ecological research (Cooke & Leishman 2011a) than earlier categorical classification (e.g. Ma, Miyake & Takahashi 2001). The plasticity of silicon accumulation within a species, explored across this special issue, complicates the development of a classification system. Questions also remain about how and why particular groups of plants have evolved but then lost the ability to accumulate Si, which can now be facilitated by genomic analysis. Stromberg's evolutionary perspective on phytolith analysis linked to phylogenies (this issue) gives a fascinating insight into Si evolution, which could be expanded to non-vascular plants.

Some gaps in our knowledge seem incredible given early ideas about likely functions for Si in plants. Si has long been suggested to have a structural and biomechanical role in plants (Raven 1983; Epstein 1994), but we still have relatively little hard evidence quantifying this (but see Dakora & Nelwamondo 2003; Schaller, Brackhage & Dudel 2012). Relationships between Si, lignin and cellulose remain unclear (Schoelynck & Struyf 2015, *this issue*), but there is increasing interest in the idea that Si could replace carbon-based structural components in plants (Raven 1983; Cooke & Leishman 2011a,b). There is some evidence of negative correlations between Si-based and C-based defences in plants (Frew *et al*. in press) and this is an area where more studies to establish general patterns are urgently needed.

This raises a more general issue of the role of climate in driving the amount, nature and type of plant defences, whether C or Si based. Long-term evolutionary patterns are intriguing, but perhaps of even more relevance are the likely impacts of more immediate global climate change. How will allocation to Si defences be affected by climate change, or conversely how can Si help protect our crops against such change? Si has an important role in protecting crops against pests and diseases (Fauteux *et al*. 2005; Guntzer, Keller & Meunier 2012; VanBockhaven, De Vleesschauwer & Höfte 2013; Reynolds *et al*. 2016), both problems projected to increase under future scenarios, but its role in alleviating abiotic stresses such as drought and salinity could become increasingly important as we seek to feed a growing population in a warming world where extreme weather could become an increasing threat to food security. Plant Si is emerging as fundamental to understanding many aspects of plant biology and the interactions between plants and other organisms, but it also offers promise to address some of the key challenges of our age.

## Final thoughts

The same four statements begin many papers in this field, including our own, describing plant Si as the second most abundant element on the earth's crust, often overlooked in plant research, comprising up to 10% of plant dry weight, and beneficial but not essential for plants. This journal issue consolidates knowledge of plant Si, demonstrating its diverse functions in ecology, irrespective of essentiality. It shows the scale on which plants impact the global Si cycle and our role in cycle modifications. Hence, we argue that we no longer need to justify our interest in plant Si and can leave stale statements behind. Let us instead stand on the shoulders of findings united in these reviews. Let us now begin papers with a statement that Si is an important element in plant biology, with complex roles in plant strategies and in mediating interactions with their environment and other organisms, and leap into new territory from here.

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